

Figure 1. Diagnostic features of the genus *Rhynchostegiopsis*. Outer surface of (a) exostome, and (b) endostome of *R. flexuosa*. —c. Stem cross section of *R. tunguraguana*. —d. Axillary hairs from *R. tunguraguana* and *R. brasiliensis*, respectively. —e. Calyptra of *R. tunguraguana*. (a, b: Morton 7395, US; c: Churchill & Sastre de Jesús 12999, MO; d: Schiffner 1454, BM, isoelectotype, and Lewis 83–710, LPB; e: Churchill & Sastre de Jesús 12999, MO.)

mosses and the implications this has on the interpretation of systematic relationships within this large group. In the mosses the gametophyte is the dominant phase of the life cycle. It was concluded that focus placed on the sporophyte alone could be misleading, and that phylogenetic relationships are more likely to be revealed by overall gametophytic correlations. Differential weight given to either gametophytic or sporophytic characters in *Rhynchostegiopsis*, in accordance with any particular classification scheme, has been important in influencing the systematic placement of the genus over time.

Utilizing mostly sporophytic features, Fleischer (1906–1908) divided the Hookeriaceae into four tribes. He placed *Rhynchostegiopsis* in his Hypnelleanae between *Sauloma* (Hook. f. & Wilson) Mitt. and *Philophyllum* Müll. Hal., based on similarities in peristome morphology. Brotherus (1925) adopted Fleischer's general systematic scheme. He maintained the same concept of the Hypnelleanae but raised it to the level of subfamily. The Fleischer-Brotherus system was primarily based on Philibert's observations of peristome morphology (see Taylor, 1962, for reference to entire series; Crosby, 1974; Buck, 1991). In contrast to the previous sporophyte-based classifications, Miller (1971) pub-

lished an overview of the Hookeriales based mainly on gametophyte morphology and using a set of 23 classification principles influenced by the work of Hutchinson (1959). This phylogenetic arrangement of the genera in the Hookeriales differed from all previous work. Miller (1971) was the first to recognize the similarity between *Rhynchostegiopsis* and *Leucomium* Mitt. The latter genus differed from *Rhynchostegiopsis* only by its entire leaf margins, lack of endostomial cilia, and sexuality. *Leucomium* is autoicous, synoicous, or polyoicous (Allen, 1987), whereas *Rhynchostegiopsis* is dioicous. *Rhynchostegiopsis* was placed in the Leucomiaceae by Miller (1971), along with *Philophyllum*, *Sauloma*, *Pulvinella* Broth. & Herzog, *Stenodesmus* (Mitt.) A. Jaeger (Miller, 1971), and the two original members of the family, *Leucomium* and *Vesiculariopsis* Broth. However, Miller gave no explanation of the concept of this newly expanded family in this paper. Allen (1987), in a revision of *Leucomium*, documented the history related to the development of the concept of this genus, the family Leucomiaceae, and the different interpretations of the systematic relationships therein. The close *Leucomium*–*Rhynchostegiopsis* relationship was supported in this work based on the overall morphological

similarity of these two genera, and they were considered to be the only members of the Leucomiaceae at that time (Allen, 1987).

Crosby (1974) published a new classification of the Hookeriaceae based on his Philibert-Dixon principle, using peristome form and subsequently gametophytic characters to group genera (Dixon, 1932; Crosby, 1974). The Philibert-Dixon principle was defined as primary weight being given to characters of the sporophyte, in particular the peristome, when constructing a classification for the mosses (Crosby, 1974). Based on this principle, mosses with similar gametophytes must not be grouped together if their sporophytes differ; instead they should be placed with mosses that have similar peristomes. The Hookeriaceae were divided into eight subgroups: the Distichophylloid, Adelotheoid, Cyathophoroid, Hookerioid, Hemiragoid, Hookeriopsoid, Pilotrichidioid, and Ephemeropsid groups (Crosby, 1974). *Rhynchostegiopsis* was placed in Crosby's Hemiragoid group along with *Hemiragis* (Brid.) Besch., *Philophyllum*, *Dimorphocladon* Dixon, and *Sauloma*. This Hemiragoid group was defined by lanceolate leaves, none or two costae, and lax laminal cells. Crosby (1974) found that within the Hookeriaceae, two characters of the peristome were variable: (1) the median line of the exostome (either furrowed or zig-zag), and (2) endostomial cilia (either present or absent). Mosses with, or mosses without, endostomial cilia did not form natural groups. It was considered that any arrangement of taxa based on either of those character states would result in groups with low overall morphological similarity (Crosby, 1974). One of the few features that differs between *Rhynchostegiopsis* and *Leucomium* is the presence of endostomial cilia found in *Rhynchostegiopsis*. In contrast to previous classifications, *Leucomium* was placed in the Hypnaceae near *Vesicularia* (Müll. Hal.) Müll. Hal. based on its cucullate calyptra and leaf areolation. However, the family Leucomiaceae was synonymized with the Hookeriaceae (Crosby, 1974). This placement of *Leucomium* in the Hypnaceae was later followed by Vitt (1984) in his classification of the Bryopsida.

Comparison of members of the Leucomiaceae to some genera of the Hypnaceae indicates that there are less than clear distinctions between these families. Both families exhibit an overlap in characters and character state variation in sporophyte and gametophyte morphology. This broad overlap in characters between the Leucomiaceae and Hypnaceae is exemplified by the genera *Rhynchostegiopsis*, *Leucomium*, and *Vesicularia*. Both *Leucomium* and *Rhynchostegiopsis* (Leucomiaceae) resemble *Vesi-*

cularia (Hypnaceae) in habit and the presence of a cucullate calyptra, but they both lack stem pseudoparaphyllia, which are typical of the Hypnaceae. All three genera are ecostate, and leaf areolation in *Leucomium* and *Rhynchostegiopsis* is similar to that of *Vesicularia*. *Vesicularia* and *Rhynchostegiopsis* both have endostomial cilia, while *Leucomium* lacks them. Discordant with the Hypnales but typical of members of Hookeriaceae, sensu Whittemore and Allen (1989), are the lack of pseudoparaphyllia and the two-celled axillary hairs of *Rhynchostegiopsis* and *Leucomium*.

In contrast to previous sporophyte-based classification systems, and that of Miller (1971), Buck and Vitt (1986) presented a familial classification of the pleurocarpous mosses based on correlated gametophytic and sporophytic characters. The Hookeriales were defined by leaves with lax areolation; costa single, but more typically absent or double; collenchymatous exothecial cells; an exostome with a median furrow; rostrate opercula; and mitrate calyptrae. The Leucomiaceae were distinguished from other families in the order by their elongate, lax leaf cells, enlarged cortical cells of the stem, and cucullate calyptrae. The family contained just three genera: *Leucomium* and *Vesiculariopsis*, following the arrangement of Brotherus (1925), and *Rhynchostegiopsis*. Buck (1987, 1988), in further rearrangements of taxa within the Hookeriales, divided the order into five families according to gametophytic characters. He considered the variation in exostome form in the Hookeriales to be an unreliable indicator of relationships both within and between families. *Rhynchostegiopsis* was retained with *Leucomium*, in his Leucomiaceae, based on gametophytic similarities. The Leucomiaceae were characterized by ecostate leaves with long-lax leaf cells; fragile stems; undifferentiated stem anatomy; a typical hookerioid peristome (except for endostomial cilia found in some taxa); and cucullate calyptrae (Buck, 1987). The characters of cucullate calyptra and undifferentiated stem anatomy of the Leucomiaceae were used to segregate it from the Hookeriaceae.

Whittemore and Allen (1989) presented a classification of the Hookeriales based on gametophyte and sporophyte morphology, recognizing only two groups within the Hookeriales, the *Hookeria* group (as the Hookeriaceae Schimp.) and the *Daltonia* group (as the Daltoniaceae Schimp.). The Leucomiaceae were placed in synonymy with their expanded Hookeriaceae. This broader concept of Hookeriaceae was defined as a taxon with branched stems; bicostate or ecostate leaves; straight rhizoids (unbranched and tightly clustered below the leaf

base); two-celled axillary hairs; and a weakly pigmented stem cortex (Whittemore & Allen, 1989).

Despite the uncertainty over the recognition of the Leucomiaceae expressed by some of the earlier-mentioned authors, the concept of this family has been developed over time. Buck (1992) placed the neotropical endemic genus *Philophyllum* in the Leucomiaceae supported by its distinctive stem anatomy, calyptra, and annular development. *Philophyllum* has calyptrae that are variable in state; they are both mitrate and cucullate. Although members of the Leucomiaceae are considered defined, in part, by cucullate calyptrae, the infraspecific variability in calyptra form in *Philophyllum* was not considered grounds for its exclusion. *Philophyllum* is similar to all other members of the Leucomiaceae in its characteristic large thin-walled stem cells. Buck (1992) noted that the stem anatomy in the Leucomiaceae was unique to this family and an important defining character of it. Although leaves in the Leucomiaceae are generally ecostate, the occasional occurrence of short, double costae in *Philophyllum* was not considered critical to exclude the genus from the Leucomiaceae (Buck, 1992). Short double costae have been reported in some specimens of *Rhynchostegiopsis tunguraguana* Buck (1998). However, in this study only traces of a bistratose leaf lamina have been seen in a few specimens indicating that the occurrence of double costae is in fact rare. These traces of a bistratose layer were seen at the very base of leaves and were only visible in cross section.

The Ptychomniaceae have cucullate calyptrae in common with the Leucomiaceae. The Ptychomniaceae were first placed in the Hookeriales, near the Hookeriaceae, by Robinson (1971). It was considered close to the Hookeriaceae and Leucomiaceae based on the furrowed exostome teeth of some of the genera, the lack of costae, and poorly developed alar cells (Robinson, 1975). Hattaway (1984), in a monograph of the Ptychomniaceae, also concluded that this family belonged in the "Hypno-bryalean" order close to the Hookeriaceae, Sematophyllaceae, or Hypnaceae, although the exact affinities of it were not fully stated. Characters of the Ptychomniaceae that differ from those of the Leucomiaceae are stem paraphyllia, colored alar cells that can be differentiated, incrassate-porose cells throughout, and ribbed capsules (Hattaway, 1984). All these features are, in fact, generally discordant with most genera in the Hookeriales, and more specifically all those in the Leucomiaceae. If the Ptychomniaceae are excluded from the Hookeriales, pending further investigation, then the Leucomiaceae are the only family in the Hookeriales with cucullate calyptrae.

The genus *Tetrastichium*, containing *Tetrastichium fontanum* (Mitt.) Cardot, was traditionally considered to be a member of the Hookeriaceae based on its short, hexagonal, lax upper leaf cells (Allen et al., 1985b). After closer examination of this species, Allen et al. (1985b) discussed the systematic placement of it. They were the first to note the similarity between *T. fontanum* and *Rhynchostegiopsis*, especially in leaf cell areolation and peristome features. The exostome and endostome of these two genera are almost identical. Another species, *Lepidopilum virens* Cardot, was later transferred to *Tetrastichium* by Churchill (1989) based on its leaf cell areolation, as well as its endostome and exostome features. Morphological characters traditionally used to align *Tetrastichium fontanum* with *Hookeria* Sm. in the Hookeriaceae included leaf cell areolation and lack of a costa. Ecostate leaves are also characteristic of the Leucomiaceae. In addition to this, *Tetrastichium fontanum* has leaf cells similar to those of *Rhynchostegiopsis brasiliensis*, the larger forms of *R. flexuosa*, and *Leucomium*. *Tetrastichium* is another genus that is variable in its calyptra form, which can be either mitrate or cucullate, a feature that it shares with *Philophyllum*. Inclusion of the genus *Tetrastichium* in the Leucomiaceae is therefore supported by leaf areolation, stem anatomy, exostome and endostome features, and its calyptra.

Hedenäs (1995) investigated relationships among the diplolepidous pleurocarpous mosses, and between the Hookeriales and Sematophyllaceae (Hedenäs, 1996b) using cladistic methods. *Rhynchostegiopsis* was not included in the data sets; however, *Leucomium* was found to be a relatively basal member of the "Hookeriales" along with *Tetrastichium virens* (Cardot) S. P. Churchill and *Tetrastichium fontanum*. In an additional paper Hedenäs (1996a) presented a set of cladistic analyses of "Hookeriales" based on 75 morphological characters of 80 species from 50 genera, this time including 1 species of *Rhynchostegiopsis*. The species *Leucomium strumosum* (Hornsch.) Mitt. and *Rhynchostegiopsis flexuosa*, and *Tetrastichium fontanum* and *T. virens* consistently formed sister clades in the analyses, supporting the proposed relationships of *Leucomium–Rhynchostegiopsis* and *Tetrastichium–Leucomium–Rhynchostegiopsis*. However, the topologies of the trees from both these sets of analyses were not well supported statistically (Hedenäs, 1995, 1996b). The separate analyses also highlighted some of the problems associated with the high levels of homoplasy within the Hookeriales and Hypnales, especially how these significant levels of homoplasy may influence results in large-

scale cladistic analyses when using large numbers of taxa and/or characters.

To date, taxonomic and floristic treatments differ in the recognition of the Leucomiaceae and positioning of *Rhynchostegiopsis* within the Hookeriales. Authors either follow the more traditional view of *Rhynchostegiopsis* aligned with the Hookeriaceae (Bartram, 1949; Crum & Steere, 1957; Crum & Bartram, 1958; Whittemore & Allen, 1989), or recognize the Leucomiaceae and the *Rhynchostegiopsis*–*Leucomium* relationship within it (Allen, 1987; Crum, 1994; Churchill & Linares, 1995; Buck, 1998). The Leucomiaceae are defined herein by ecostate or sometimes bicostate leaves; lax leaf cells; stems composed of large thin-walled cells throughout; collenchymatous exothecial cells; rostrate opercula; striate-furrowed exostome teeth; a well-developed endostome, with or without cilia; and cucullate or mitrate calyptrae. It is clear that *Rhynchostegiopsis* belongs in the Leucomiaceae, along with *Leucomium*, *Philophyllum*, and *Tetrastichium* (Mitt.) Cardot, based on the overall sporophytic and gametophytic characters they share and that define the Leucomiaceae. Other genera that were traditionally placed in the Leucomiaceae have been transferred to other families, mainly the Pilotrichaceae (*Vesiculariopsis*, *Sauloma*, and *Stenodesmus*).

MORPHOLOGICAL VARIABILITY IN *RHYNCHOSTEGIOPSIS*

Study of over 400 herbarium specimens allowed for morphological variability in the genus to be assessed throughout its geographic range. Species were identified using measurements of leaf cell length, leaf size, and stem size combined with leaf shape, apex length and shape, and upper leaf margin form. *Rhynchostegiopsis* is a difficult genus because there are few characters that define it, and its characters can vary continuously within and between species. Variation within species is not obvious when comparing only type specimens or the typical forms of each taxon. However, often striking differences in plant form, size, and leaf morphology emerge when examining a large number of specimens. As a result of the variability in characters as well as the wide range of variation seen within species of *Rhynchostegiopsis*, the circumscription of them is difficult. Critical examination of leaves from different positions on each plant may be required for identification purposes.

Character variations in *Rhynchostegiopsis* often appear to be independent of the other characters, and their states, for a particular species. For any

given species, specimens that may be unusual in one character have other characters typical for that species. *Rhynchostegiopsis* grows in moist and humid habitats. Morphological differences can be seen when plants are found growing on different substrates and under presumably different environmental regimes. Such variability has also been attributed to environmental influences in other genera of the Hookeriales, *Leucomium* (Allen, 1987), *Pilotrichidium* Besch. (Allen & Crosby, 1986), *Stenodictyon* (Allen et al., 1985a), and *Philophyllum* (Buck, 1992).

PHYTOGEOGRAPHY

Rhynchostegiopsis is endemic to the Neotropics. One species, *Rhynchostegiopsis brasiliensis*, is especially limited in distribution, as it is known only from three localities in southeastern Brazil (represented by the triangle in Fig. 2). The other species are found in Mexico, Central America, the Caribbean, and the northern and central Andes. This tropical Andes–southeast Brazil disjunct distribution pattern is found frequently in mosses (Buck, 1990), including the closely related genus *Leucomium* (Allen, 1987). *Rhynchostegiopsis tunguraguana* is the most geographically widespread of the species and is found from Mexico through Central America to northern South America and Bolivia (Fig. 2). No collections of *R. tunguraguana* have been seen from Peru, but this is probably due to a lack of collecting rather than its absence from Peru. In the Caribbean, *R. tunguraguana* is known only from Jamaica and the Dominican Republic.

The most frequently collected species, *R. flexuosa*, is almost entirely restricted to Central America and the Caribbean. In South America *R. flexuosa* is known from two collections in Colombia (Steere 7688a and 7671) (Fig. 3a). Widespread in the Caribbean, *R. flexuosa* is found on almost all the islands from Cuba to Trinidad. The remaining species, *R. costaricensis* and *R. carolae*, are narrow Central American endemics (Fig. 3b and c, respectively). They are both known from Costa Rica with one locality in Honduras for *Rhynchostegiopsis costaricensis*, and one locality in Panama for *Rhynchostegiopsis carolae*.

MATERIALS AND METHODS

This revision is based on 406 specimens from BM, DUKE, F, H, H-BR, LPB, MO, NY, and US. All specimens examined were entered into the TROPICOS–MOST database at Missouri Botanical Garden (<http://www.mobot.org>). Locality information and coordinates were included with each spec-

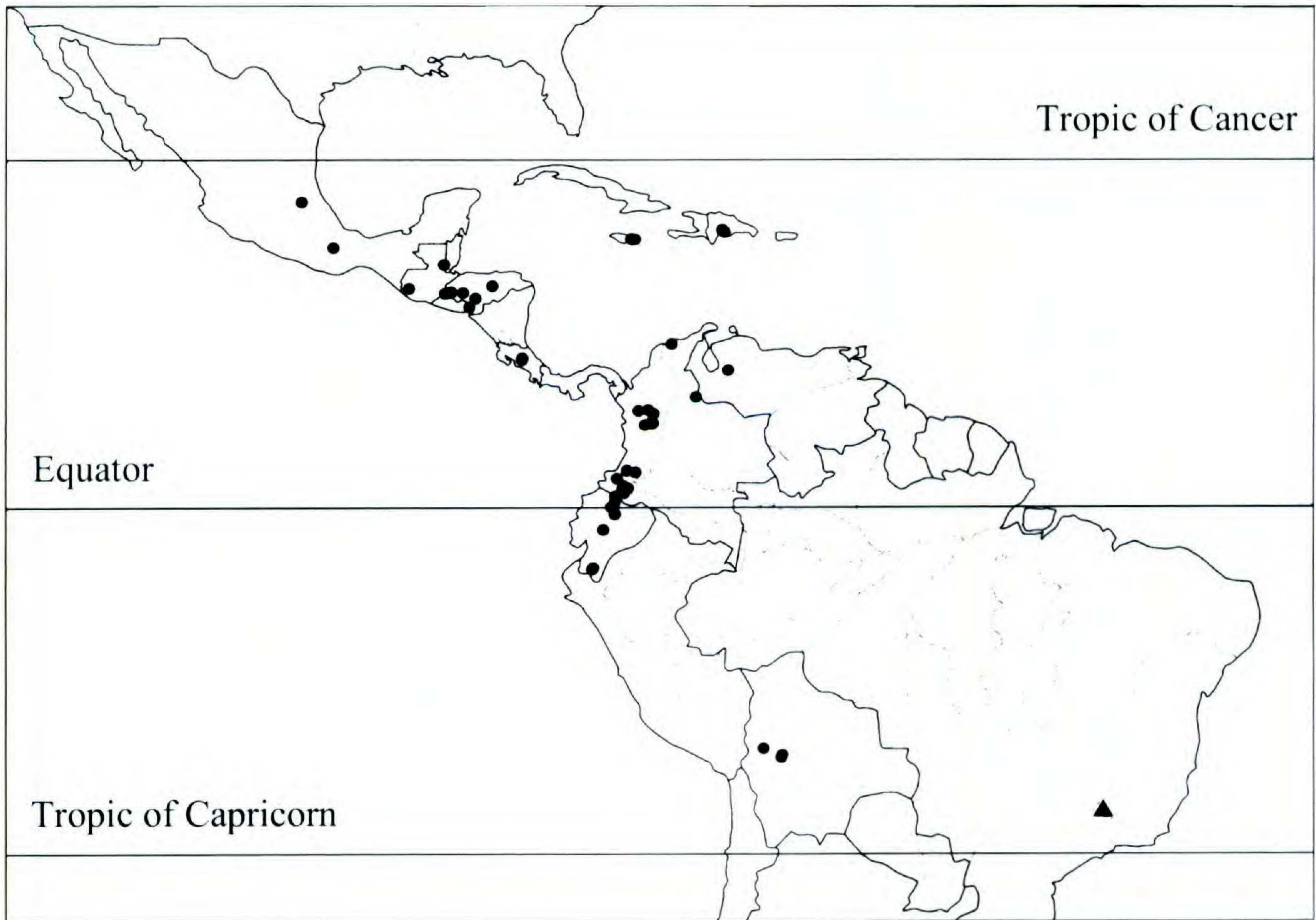


Figure 2. Distribution of *Rhynchostegiopsis brasiliensis* (triangle) and *Rhynchostegiopsis tunguraguana* (circles).

imen entry. Mapping was done using ArcView GIS (ESRI, 1998). Coordinates for localities were extracted from the TROPICOS–MOST database, and distribution maps are based on the herbarium specimens examined during this study. The sections on “selected specimens examined” include one collection per political subdivision (province) for each country. The complete list of examined specimens is available in Appendix 1 or through Internet access to the TROPICOS–MOST database. Specimens were examined in aqueous and Hoyer’s solution mounts (Anderson, 1954), with cell measurements taken from Hoyer’s solution mounts. Leaf width is measured at mid-leaf. Measurements of the setae include the vaginula. Cell measurements include the cell wall. Marginal cells refer to the outermost row of cells of the leaf lamina. Median cells refer to the cells that are central in the leaf.

TAXONOMIC TREATMENT

Rhynchostegiopsis Müll. Hal., *Nuovo Giorn. Bot. Ital.* n.s. 4: 163: 1897, as “tribus.” TYPE: *Rhynchostegiopsis complanata* Müll. Hal.

Plants small to large, 10–120 mm long, glossy, pale or dark green to yellow-green or golden with age; forming dense to thin mats. *Stems* fragile to sturdy, sometimes dark colored, creeping or spread-

ing, sub-pinnately to irregularly branched, complanate-foliate; in cross section cells homogeneous, large and thin-walled, central strand absent, hyalodermis lacking; paraphyllia and pseudoparaphyllia absent; axillary hairs two-celled, basal cell short-cylindrical, small, brown, upper cell long-cylindrical, enlarged, hyaline; *rhizoids* dark red, smooth, clustered on underside of stem, at base of and below leaf insertions. *Leaves* spreading, sometimes falcate, usually crowded, not much contorted wet or dry, sometimes longitudinally folded; lanceolate, oblong-lanceolate, ovate or ovate-lanceolate, plane to slightly concave below, plane above, apices short- to long-acuminate, straight or flexuose; symmetric, not decurrent; lateral, dorsal, and ventral leaves somewhat differentiated, lateral and dorsal leaves smaller; lamina unistratose; margins entire below, sharply serrate, serrate, or serrulate above, sometimes sub-entire in some leaves; ecostate; laminal cells smooth, walls non-porose; median leaf cells lax to firm, long-linear to long-hexagonal throughout; alar cells not differentiated; basal cells slightly broader and shorter than median cells, sometimes differentiated in association with leaf gemmae; upper marginal cells conspicuously or slightly enlarged in comparison to median cells. *Asexual reproduction* none or by leaf gemmae, gemmae in distinct clusters on dorsal leaf surface, or

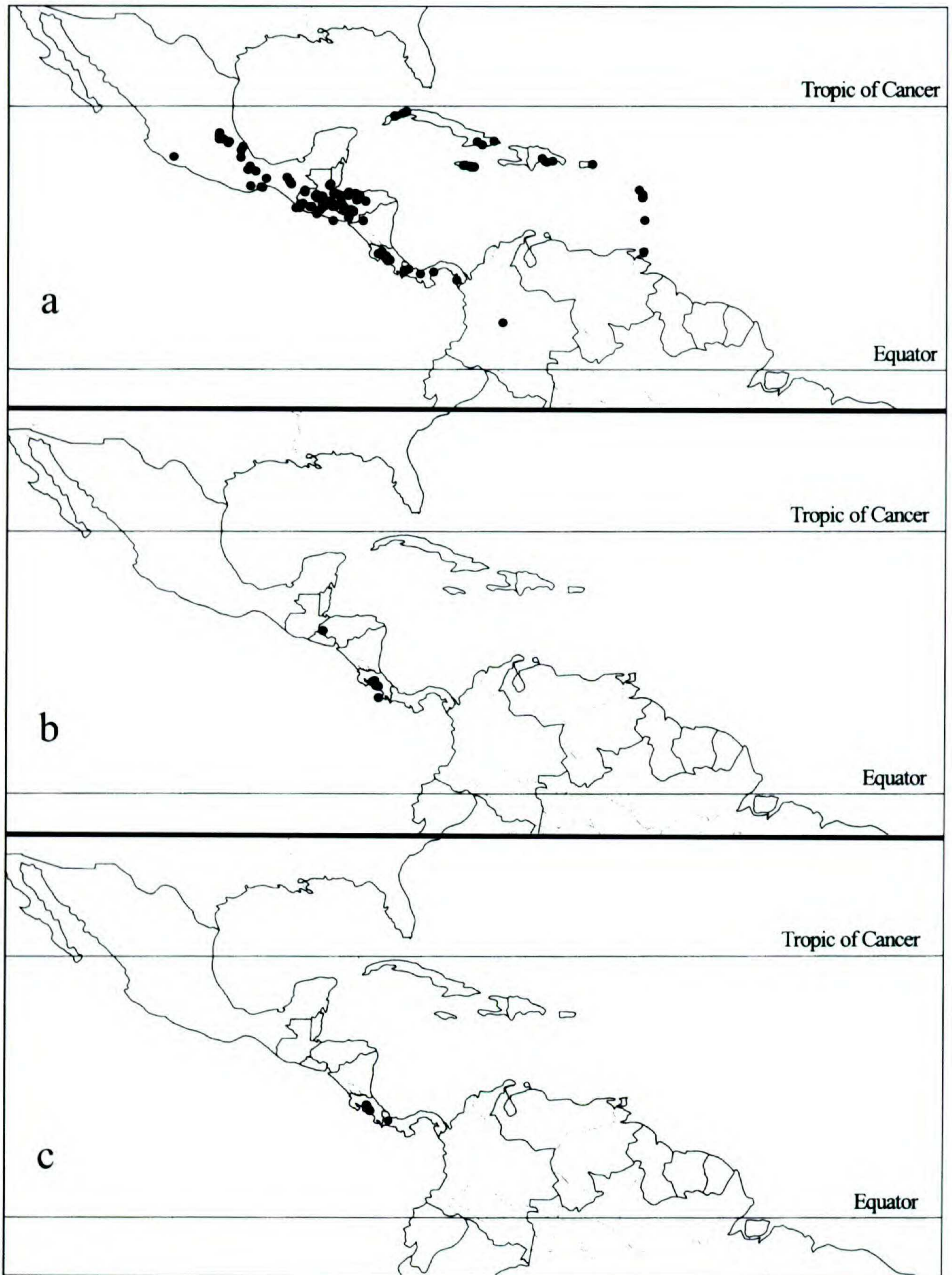


Figure 3. Distribution of (a) *Rhynchosegiopsis flexuosa*, (b) *Rhynchosegiopsis costaricensis*, and (c) *Rhynchosegiopsis carolae*.

on the stem at leaf base. *Dioicous*. *Perigonia* lateral, leaves smaller than but otherwise similar to perichaetial leaves. *Perichaetia* lateral, conspicuous or inconspicuous; leaves erect with spreading apices, ovate to ovate-lanceolate, apices sub-entire to serrate, sometimes flexuose; ecostate; median cells long-hexagonal to long-linear; basal cells

shorter and broader than median cells; alar cells not differentiated. *Setae* solitary, long, smooth to sometimes roughened just below base of capsule, reddish to dark red. *Capsules* exserted, inclined to horizontal or pendent; *urn* cylindrical, smooth, neck undifferentiated; exothecial cells sub-quadrate to short-rectangular, collenchymatous with horizontal

walls usually thicker than vertical walls; stomata at base of urn, superficial; *opercula* long-rostrate from a conic base; *annuli* 2–5 layers of thin-walled cells, deciduous. *Peristome* double, exostome teeth 16, narrowly triangular, finely papillose above, densely horizontally striate with narrow median line below; endostome basal membrane high, segments 16, narrowly triangular, almost as long as exostome teeth, keeled, smooth to finely papillose, often narrowly perforate, cilia 1 to 2(3), well developed. *Calyptrae* long cucullate, often split from the base 2/3 of length, smooth. *Spores* spherical, 11–20 μm diam., finely papillose.

Etymology. *Rhynchostegiopsis* was derived from the generic name *Rhynchostegium* Bruch & Schimp., “*opsis*” meaning resembling, in reference to the similarity of its rostrate opercula to that of the genus *Rhynchostegium*. The name *Rhynchostegium* was derived from the Greek “*rhychos*,” meaning beaked, and “*stegē*,” meaning cap or cover, in reference to the shape of its opercula.

Distribution. Central America (all countries from Mexico to Panama), the Caribbean (Cuba, Jamaica, Puerto Rico, Dominican Republic, Leeward and Windward Isles), and South America (Venezuela, Colombia, Ecuador, Bolivia, and southeastern Brazil) (Figs. 2, 3).

Ecology. Inhabiting montane forests from middle to high elevations. On trunks, roots, and branches of living trees, on fallen decayed logs and soil or leaf litter in moist, humid habitats.

Discussion. The name *Rhynchostegiopsis* was first invalidly published, as a section, in a description of a new species, *Vesicularia auricolor* Müll. Hal. (as *Vesicularia (Rhynchostegiopsis) auricolor*) (Müller, 1897a). *Rhynchostegiopsis* was established, in a slightly later publication, for the newly described *R. complanata* Müll. Hal. from Bolivia (Müller, 1897b). Two species, *Hypnum flexuosum* Sull. and *Vesicularia auricolor*, were transferred from their respective genera into the new genus *Rhynchostegiopsis* in the later publication (Müller, 1897b). A formal generic description of *Rhynchostegiopsis* was lacking in the original publication (Müller, 1897b), and the description of *R. complanata* cannot be used in its place because the genus was not monotypic when published. Instead, a small diagnosis of a “tribus” in the original (1897b) publication has been traditionally accepted as the generic description of *Rhynchostegiopsis* (Welch, 1966). This diagnosis by Müller (1897b) succinctly describes *Rhynchostegiopsis* as having serrate, ecostate leaves with lax pellucid leaf cells, a bent, fine leaf apex, and a rostrate operculum.

KEY TO THE SPECIES OF *RHYNCHOSTEGIOPSIS*

1. Plants up to 30(–40) mm long; leaves 1.0–2.5 mm long, 0.2–0.9 mm wide 2
- 1'. Plants up to 100(–120) mm long; leaves 1.7–7.0 mm long, 0.7–2.1 mm wide 4
- 2(1). Leaf apices short-acuminate 1. *R. brasiliensis*
- 2'. Leaf apices long-acuminate 3
- 3(2). Leaf apices flexuose, sharply serrate, serrate or serrulate, marginal cells larger than median cells, forming a distinct border; gemmae none 4. *R. flexuosa*
- 3'. Leaf apices not flexuose, serrate, serrulate to sub-entire, marginal cells undifferentiated, not forming a distinct border; gemmae frequent, on dorsal surface of leaf 3. *R. costaricensis*
- 4(1). Leaves 1.7–4.6 mm long, 0.7–1.6 mm wide, margins serrate or serrulate 5. *R. tunguraguana*
- 4'. Leaves 4.5–7.0 mm long, 1.5–2.1 mm wide, margins serrulate or sub-entire 2. *R. carolae*

1. *Rhynchostegiopsis brasiliensis* Broth., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 83: 339. 1927. TYPE: Brazil. São Paulo: “In silvaticus prope Barra Mansa in districtu urbis Itapecirica, ad arbores, ca. 1000 m.” *V. Schiffner 1454* (lectotype, here designated, H-BR!; isolectotype, BM!). Figure 4.

Plants small, pale yellow-green, growing in compact mats. *Stems* 10–30 \times 1–2 mm, often fragile, creeping, somewhat complanate-foliate, branching frequently, irregularly pinnate; *rhizoids* infrequent. *Leaves* not much contorted wet or dry, spreading, somewhat falcate, evenly spaced, ovate, 1.0–1.5 \times 0.4–0.6 mm, slightly concave below, plane above; apices short-acuminate; margins entire below, serrate to weakly serrulate above, sometimes almost entire; upper marginal cells mostly larger or only slightly larger than adjacent median cells; median leaf cells long-hexagonal, 80–137 \times 12–17 μm ; basal cells broader and shorter than median cells, 62–100 \times 22–29 μm . *Asexual reproduction* unknown. *Perigonia* not seen. *Perichaetia* and *sporophytes* not seen.

Etymology. Named after Brazil, the country of the type collection.

Distribution. *Rhynchostegiopsis brasiliensis* is known only from southeastern Brazil (Fig. 2). Elevation 800–1000 m.

Ecology. On trees.

Discussion. This species is distinctive in its small size combined with its ovate leaves with short-acuminate apices. *Rhynchostegiopsis brasiliensis* is similar in size and habit to *R. flexuosa*, but the latter species is distinguished by its broader leaves with short-acuminate, straight leaf apices and shorter, more hexagonal median leaf cells. In leaf shape it resembles some of the Central Amer-

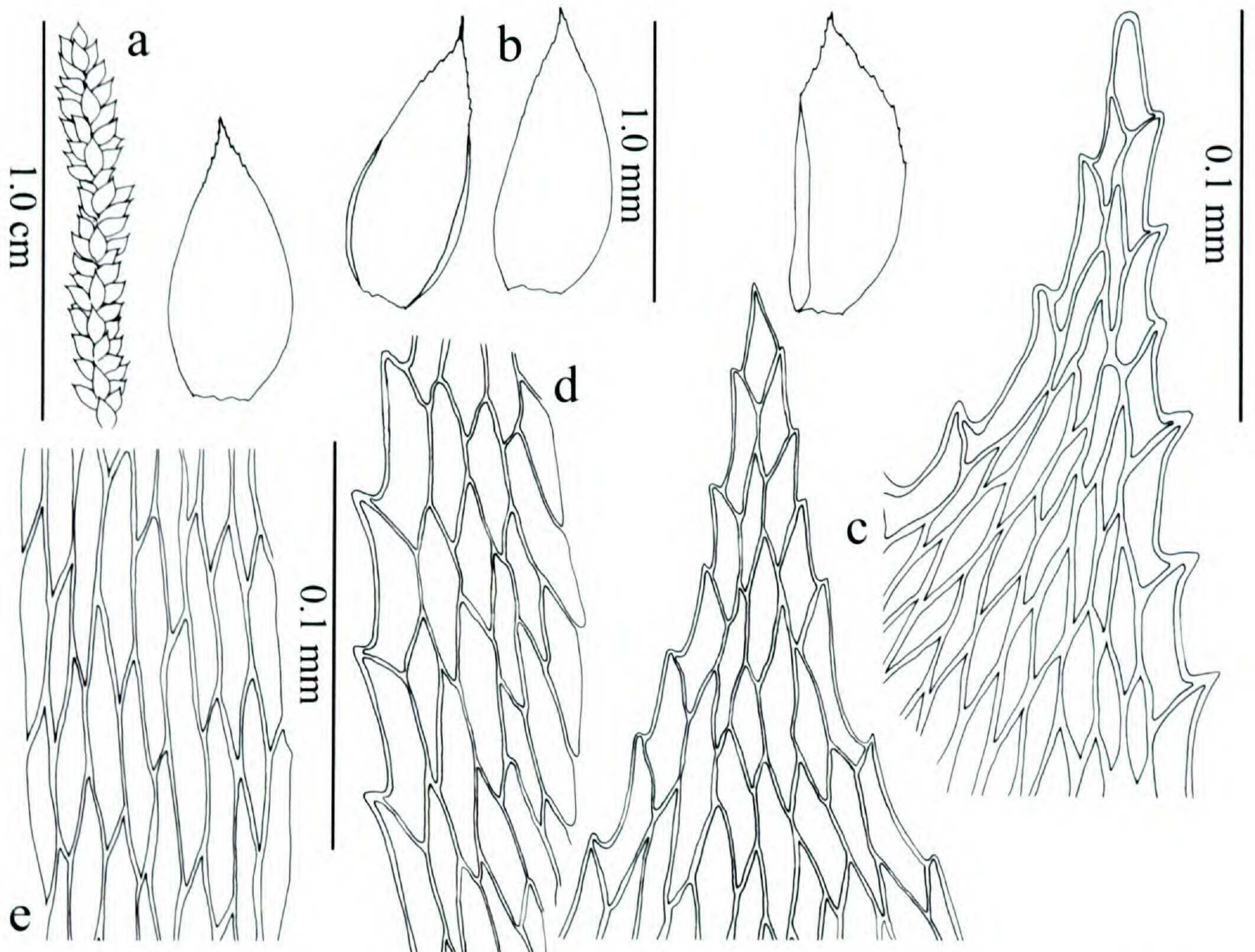


Figure 4. *Rhynchoslegiopsis brasiliensis*. —a. Portion of stem. —b. A selection of leaves. —c. Leaf apices. —d. Leaf margin. —e. Median cells. (a, c–e: Schiffner 1454, BM, isolectotype; b: Schiffner 1454, 679, 1122, BM.)

ican specimens of *R. tunguraguana*, which can often have ovate leaves with short leaf apices, but it is easily distinguished by its much smaller size and wider, shorter leaf cells. Leaf margins in *R. brasiliensis* can vary from sharply serrate to almost entire, often on the same plant. This species may be mistaken for *Vesicularia* by its aspect but belongs in *Rhynchoslegiopsis*, and not *Vesicularia*, because of the presence of two-celled axillary hairs and lack of pseudoparaphyllia on the stems. *Vesicularia* has foliose pseudoparaphyllia and axillary hairs that consist of a short brown basal cell and several elongate, hyaline upper cells. Gemmae, perichaetia/perigonia, and sporophytes are so far unknown in *R. brasiliensis*. Despite the lack of sporophyte material to confirm peristome characters, the position of this species in *Rhynchoslegiopsis* is supported by the gametophyte features, especially stem anatomy and the lack of stem pseudoparaphyllia. *Rhynchoslegiopsis brasiliensis* is currently known only from three localities around São Paulo, Brazil. In the bryophyte herbarium at MO, no further collections of this species were found among the unnamed material of *Vesicularia* or among the Hypnaceae or Hookeriaceae from Brazil.

Selected specimens examined. BRAZIL. **São Paulo:** In silvis ad “Brasso grande” in districtu urbis Itapeirica, ad arbores, ca. 1000 m, V. Schiffner 1122 (syntypes, H-BR, BM); Prope Rio Grande ad “São Paulo Railway” ad arbores, 800 m, V. Schiffner 679 (syntype, BM).

2. *Rhynchoslegiopsis carolae* Crosby, Ann. Missouri Bot. Gard. 63: 373, f. 1–5. 1976 [1977]. TYPE: Costa Rica. San José: along Inter-American Highway, 13 km SE of El Empalme, 09°40'N, 83°51'W, 2600 m, 15 Mar. 1973, M. R. Crosby & C. A. Crosby 5836 (holotype, MO!; isotypes, BA not seen, BM!, CR not seen, DUKE!, H not seen, MICH not seen, NICH not seen, NY!, US!). Figure 5.

Plants large, robust, pale green to yellow-green to golden with age, forming thin mats. *Stems* 50–100(–120) × 5–7 mm, creeping, complanate-foliate, infrequently sub-pinnately branched. *Leaves* slightly differentiated, dorsal leaves smaller than lateral leaves, evenly spaced, not crowded, not much contorted wet or dry, weakly complanate, erect-spreading, somewhat falcate, ovate-lanceolate, 4.5–6.0 × 1.5–2.1 mm, slightly concave below, flat above, apices long-acuminate; margins en-

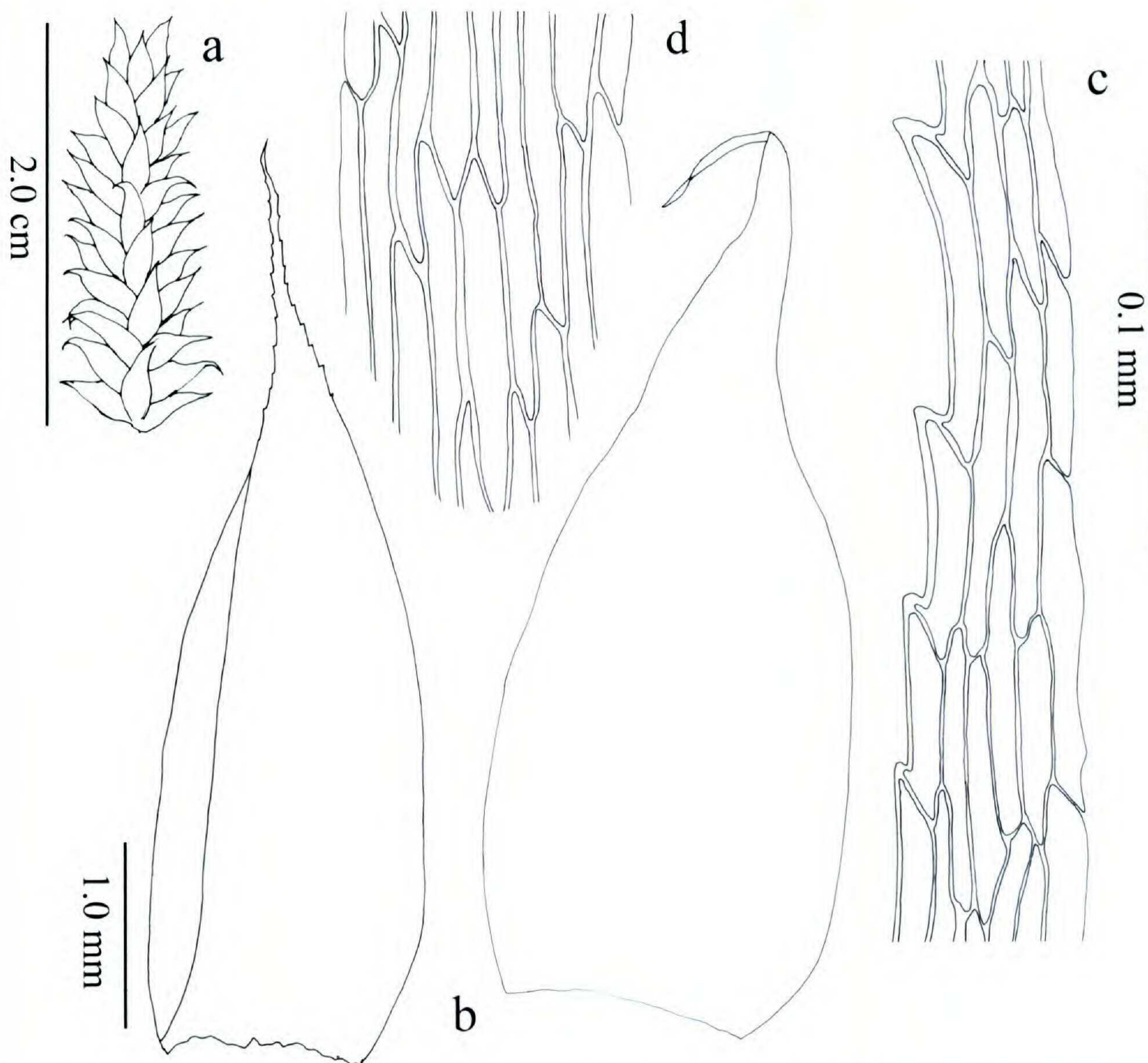


Figure 5. *Rhynchostegiopsis carolae*. —a. Portion of stem. —b. Leaves. —c. Leaf margin. —d. Median cells. (a–d: Crosby 5836, MO, holotype.)

tire below, weakly serrulate to sub-entire above; median cells long-hexagonal or long-linear, $125\text{--}290 \times 11\text{--}27 \mu\text{m}$; basal cells wider than but otherwise not much differentiated from median cells, $82\text{--}215 \times 35\text{--}57 \mu\text{m}$; upper marginal cells only weakly or not enlarged in comparison to median cells, $82\text{--}175 \times 6\text{--}16 \mu\text{m}$. *Asexual reproduction* unknown. *Perigonia* inconspicuous, leaves 0.8–1.6 mm, otherwise similar to perichaetial leaves. *Perichaetia* inconspicuous, leaves 1.5–2.3 mm, mostly ovate, gradually long-acuminate, apices entire or weakly serrulate. *Setae* 16–41 mm, smooth, dark red. *Capsules* inclined; *urn* cylindrical, $1.5\text{--}2.0 \times$ to 1 mm; *annuli* not seen; *opercula* long-rostrate, 1.4–1.6 mm; *exostome teeth* 650–750 μm . *Calyptrae* to 2 mm. *Spores* 13–20 μm diam.

Etymology. Named after one of the collectors, Carol A. Crosby, daughter of L. E. Anderson.

Illustrations. Crosby (1976), figures 1–5.

Distribution. Costa Rica, Panama (Fig. 3c). Elevation 1400–2680 m.

Ecology. Moist and shaded terrestrial habitats such as road banks, ravines, and drainage ditches in montane forests.

Discussion. *Rhynchostegiopsis carolae* is distinct in its very large size and large leaves combined with the only slightly enlarged marginal cells in the upper leaf apex. In this species the leaves are not as crowded as those in *R. tunguraguana*, and they tend to be flattened along the stem. Large specimens of *Rhynchostegiopsis tunguraguana* can approach *R. carolae* in size, and leaf cell measurement can overlap; however, *Rhynchostegiopsis carolae* can be distinguished by its wider stems and larger, moderately spaced leaves with weakly serrulate to almost entire margins. It is presently known only from mid elevations (1400–2680 m) in central Costa Rica and from one locality in Panama.

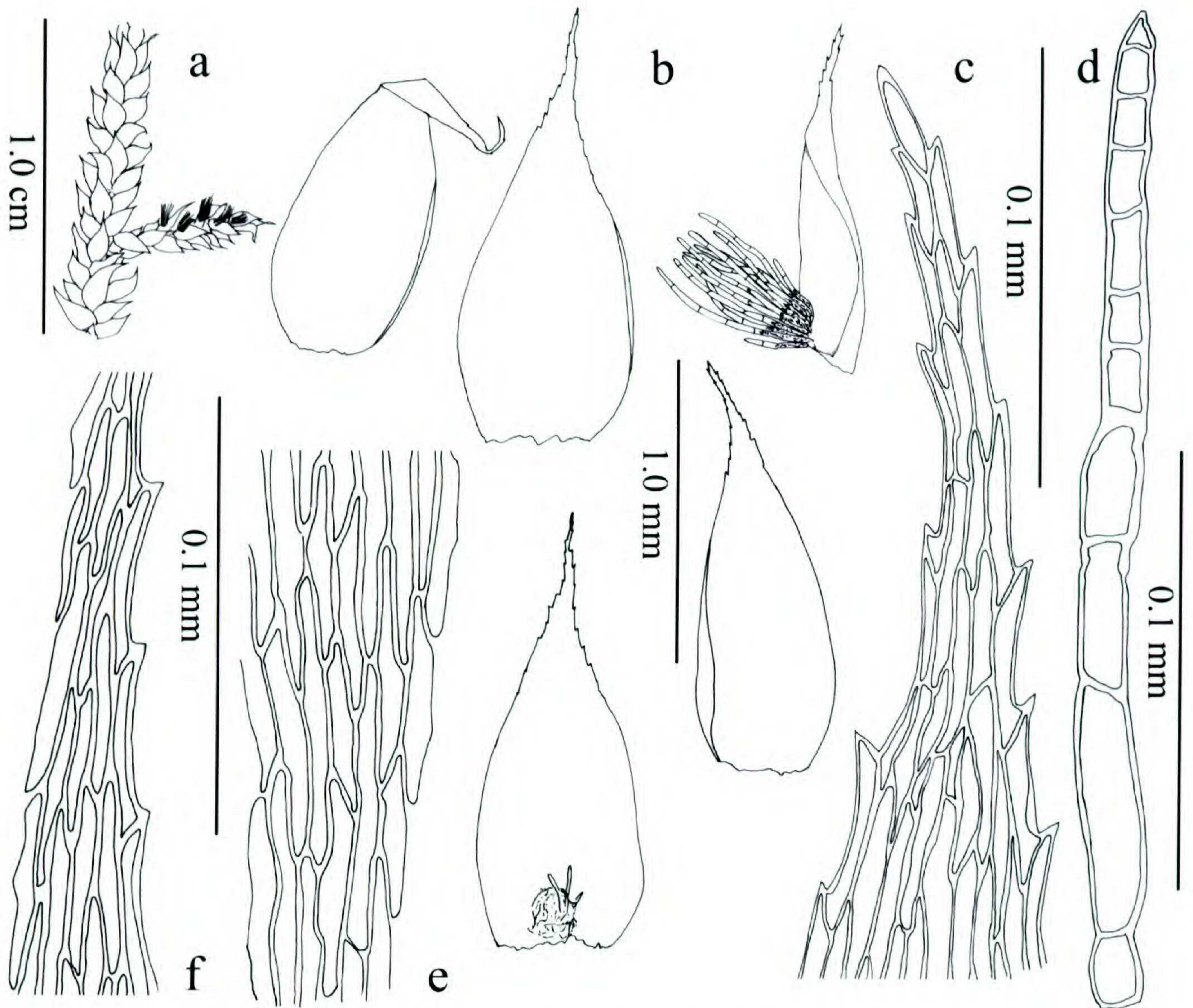


Figure 6. *Rhynchostegiopsis costaricensis*. —a. Portion of stem. —b. Leaves with and without leaf gemmae. —c. Leaf apex. —d. A leaf gemma. —e. Median cells. —f. Leaf margin. (a, c–e: *Morales 38*, US; b, f: *Crosby 9754*, MO.)

Selected specimens examined. COSTA RICA. **Cartago:** Dos Amigos, 2680 m, *Crosby & Crosby 5957* (MO). **Heredia:** Las Vueltas, 2100 m, *Crosby & Crosby 6008* (MO). **San José:** 17 km SE of El Empalme, 2650 m, *Crosby 10861* (MO). PANAMA. **Chiriquí:** Cerro Colorado, 1400 m, *Antonio 1432* (MO).

3. *Rhynchostegiopsis costaricensis* H. Rob. & D. G. Griffin, *Phytologia* 30: 281. 1975. TYPE: Costa Rica. Alajuela: Parque Nacional Volcán Poás, *Clusia* forest, E rim of crater, 2450 m, 3 Sep. 1973, *D. G. Griffin, III 92* (holotype, US!; isotype, FLAS not seen). Figure 6.

Plants small to medium, pale yellow to yellow-green; forming sparse mats. *Stems* 10–40 × 1–2 mm, often fragile, creeping, infrequently sub-pinnately branched. *Leaves* not much differentiated when dry, sometimes folded when wet, erect spreading, sometimes slightly complanate or falcate with leaf apices pointing to substrate, distant, slightly dimorphic, ovate to ovate-lanceolate, 1.0–2.4 × 0.4–0.9 mm, leaves concave below, plane

above, short- to long-acuminate; margins entire below, serrulate or sub-entire above; upper marginal cells not or slightly larger than median cells, 50–90 × 6–11 μm; median cells long-linear to long-hexagonal, 90–155 × 8–15 μm; basal cells usually shorter and broader than median cells, 65–140 × 20–40 μm, sometimes differentiated in 2–4 rows or a triangular patch at base of leaves in association with leaf gemmae, differentiated cells thick-walled. *Asexual reproduction* frequent, leaf gemmae clustered at base of leaf on dorsal surface of upper stem leaves, prominent, dark reddish at base, hyaline, fragile above, 8–15 cells long. *Perigonia* not seen. *Perichaetia* lateral, leaves 0.7–1.2 mm, short- or long-acuminate from an ovate base, apices erect to spreading, margins serrulate to sub-entire. *Setae* 9–25 mm, smooth, reddish to dark red. *Capsules* inclined; *urn* ovoid-cylindrical, 1–2 × 1 mm; *annuli* not seen; *opercula* long-rostrate, 1.2 mm; *exostome teeth* 350–500 μm. *Calyptrae* 1.6–3.0 mm. *Spores* not seen.

Etymology. Named after Costa Rica, the country of the type collection.

Illustrations. Robinson and Griffin (1975).

Distribution. Honduras, Costa Rica (Fig. 3b). Elevation 2480–3130 m.

Ecology. On rotting logs, leaf litter, or on soil, less frequently as an epiphyte on trunks or twigs of living trees.

Discussion. This species is readily distinguished from all other species in *Rhynchostegiopsis* when leaf gemmae are present. The gemmae form “tufts” on the dorsal surface of the leaves that are visible with the naked eye. Although gemmae production is not species specific in this genus, their development from the dorsal leaf surface is unique to *R. costaricensis*. Gemmae have been observed at the leaf base in the type specimen of *R. tunguraguana* (Spruce 1048, NY), and in one other collection of the same species (Ramírez 9039, NY). In these specimens the gemmae were more loosely aggregated and less well developed than those in *R. costaricensis*. They were derived from the stem tissue at the very base of the leaf rather than on the dorsal leaf surface as in *R. costaricensis*. *Rhynchostegiopsis costaricensis* can be difficult to distinguish from other species in the absence of leaf gemmae. In size and habit it could be confused with the more robust forms of *R. flexuosa*. The straight, serrulate to sub-entire apices, marginal cells that are similar in size to adjacent median cells, and its more ovate to ovate-lanceolate leaves distinguish it from *R. flexuosa*. The long-acuminate, straight apices, serrulate leaf margins, marginal cells that are similar in size to adjacent median cells, and the narrow median cells are similar to some specimens of *R. tunguraguana*. These two species can be difficult to separate based on these characters alone. The leaves in *R. costaricensis* are more distant on the stems and are smaller with shorter, narrower median and upper marginal cells.

One feature that occurs sporadically in specimens of *R. costaricensis* is the presence of an area of differentiated cells at the base of the leaf. These differentiated cells are broader and longer with much thicker walls than the cells in other leaves in the equivalent position. These differentiated cells are found in 2–4 rows or as a triangular patch at the leaf base. This “patch” of cells is described in more detail by Robinson and Griffin (1975). These differentiated cells are found on leaves that have leaf gemmae, but they can often be found on leaves even if gemmae are not present. Sporophytes are not common in these specimens, but they have been found in species that also have leaf gemmae.

Selected specimens examined. HONDURAS. **Lempira:** Parque Nacional de Celaque, 2480 m, Allen 11470 (MO). COSTA RICA. **Alajuela:** Parque Nacional Volcán Poás, 2520 m, Araya et al. 81 (F, MO, NY, US). **Cartago:** just SE of summit of Cerro de la Muerte ridge, 3050 m, Crosby 9789 (MO). **Heredia:** SW slopes of Volcán Barba, 2500 m, Crosby 13128 (MO). **San José:** 10 km NW of summit at La Ascensión, 3130 m, Crosby & Crosby 6117 (MO).

4. *Rhynchostegiopsis flexuosa* (Sull.) Müll. Hal., Nuovo Giorn. Bot. Ital. n.s. 4: 163. 1897. *Hypnum flexuosum* Sull., Proc. Amer. Acad. Arts 5: 288. 1861. *Leucomium flexuosum* (Sull.) Mitt., J. Linn. Soc., Bot. 12: 501. 1869. TYPE: Cuba. Locality not indicated, [1856B58] C. H. Wright 112 (holotype, FH not seen; isotypes, BM!, H-BR!, NY!). Figure 7.

Rhynchostegium cupressinum Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 250. 1872. *Rhynchostegiopsis cupressina* (Besch.) Cardot, Rev. Bryol. 38: 104. 1911. TYPE: “Mexico. Cordova,” C. Sallé s.n. (Sallé in herb. Decaisne) (holotype, PC not seen [in herb. of Decaisne]; isotypes, BM!, NY!).

Leucomium serratum Besch., J. Bot. (Morot) 8: 179. 1894. *Rhynchostegiopsis serrata* (Besch.) Broth., in Engl. & Prantl, Nat. Pflanzenfam. I(3): 948. 1907. TYPE: “Guadeloupe. Route du Gommier, sur les troncos pourris,” Ed. Marie 652 (lectotype, designated here, BM!; isolectotype, NY!). Ed. Marie 664 (syntypes, BM!, NY!).

Vesicularia auricolor Müll. Hal., Bull. Herb. Boissier 5: 211. 1897. *Rhynchostegiopsis auricolor* (Müll. Hal.) Broth., in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 11: 263. 1925. TYPE: “Guatemala. Alta Verapaz: Pansamala, 30 Jan. 1886,” H. v. Türckheim s.n. (holotype, H-BR!; isotypes, BM!, NY!).

Plants small to medium, bright green to yellow-green, growing in compact or thin mats. *Stems* 10–30(–40) × 1–3 mm, often fragile, creeping, irregularly to sub-pinnately branched. *Leaves* spreading to erect-spreading, somewhat complanate-foliate, falcate, or falcate-secund, often with leaf apices pointing downward, usually crowded, sometimes distant, variously to not folded when dry or wet, sometimes slightly dimorphic, lanceolate to oblong-lanceolate, 1.0–2.5 × 0.2–0.6 mm, plane or slightly concave below, plane above; apices gradually long-acuminate, flexuose; margins entire below, sharply serrate to serrulate above, upper marginal cells larger than median cells, 100–150 × 18–25 μm; median cells long-linear to long-hexagonal, 100–130 × 12–20 μm; basal cells long-hexagonal, shorter than median cells, 62–82 × 15–17 μm. *Asexual reproduction* unknown. *Perigonia* lateral, leaves similar to perichaetial leaves. *Perichaetia* conspicuous, leaves lanceolate, 0.7–1.5 mm, apices long-acuminate, spreading, usually flexuose, margins serrate to sub-entire. *Setae* 10–30 mm, dark

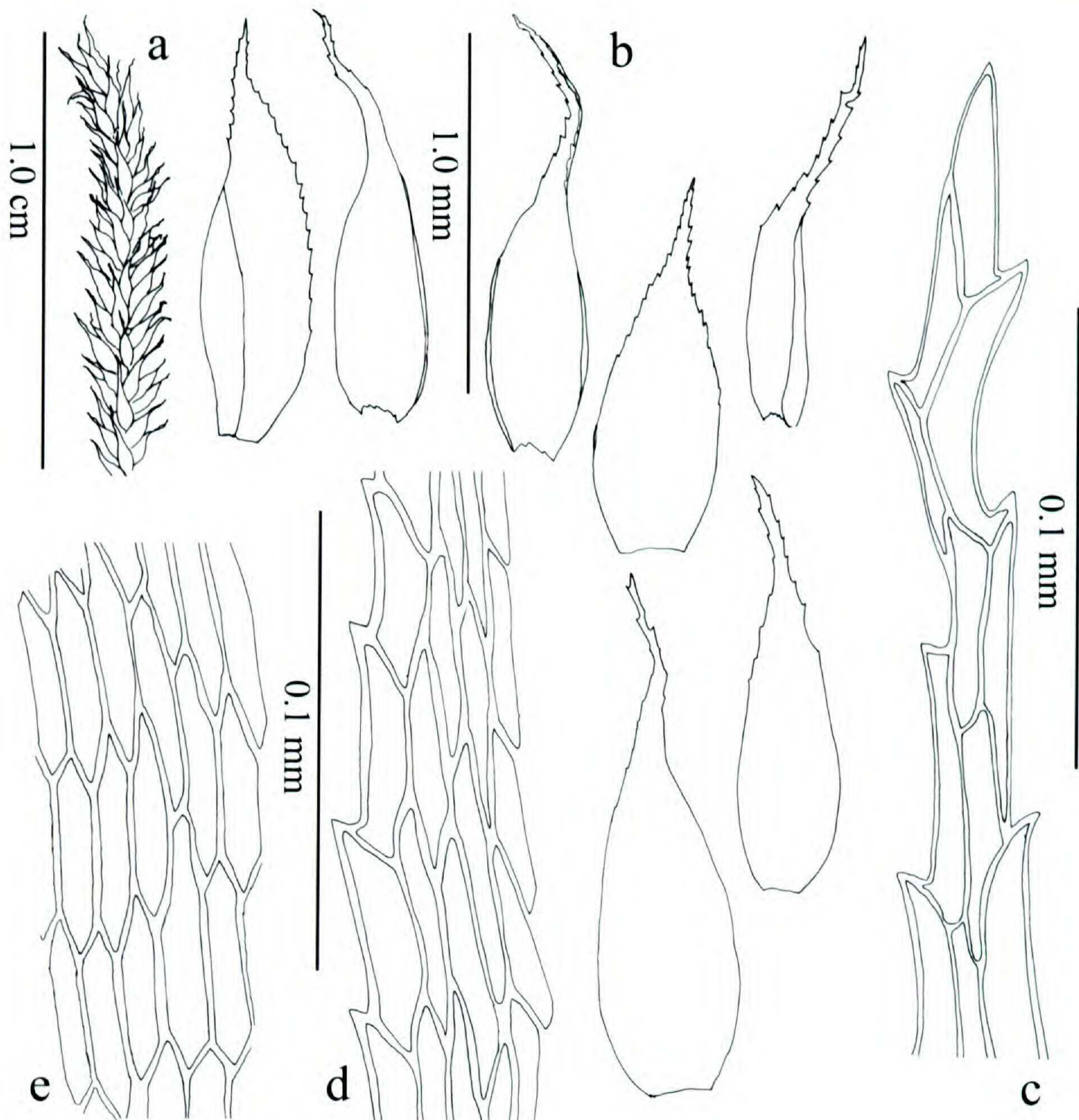


Figure 7. *Rhynchostegiopsis flexuosa*. —a. Portion of stem. —b. A selection of leaves. —c. Leaf apex. —d. Leaf margin. —e. Median cells. (a, c–e: Wright 112I, BM, isotype; b: Wright 112, BM, isotype, Price 834, MO, Allen 11959, MO, Buck 7909, NY, Pringle 10481, BM.)

reddish to orange, smooth or sometimes slightly roughened just below urn. *Capsules* inclined to pendent; *urn* cylindrical, 0.8–1.3 × 0.4–1 mm; *annuli* 2–5 layers of thin-walled cells, deciduous; *opercula* long-rostrate, 1.0–1.2 mm; *exostome teeth* 300–325 μm . *Calyptrae* 1.0–1.6 mm. *Spores* 11–15 μm diam.

Etymology. Derived from the Latin “*flexuosus*,” meaning bent alternately in opposite directions in reference to the distinctive leaf apices.

Illustrations. Bartram (1949), figure 143; Crum and Bartram (1958), figure 629; Welch (1966), figures 288–292; Welch (1972), figures 261–267; Buck (1998), plate 37.

Distribution. Mexico, Central America, the Caribbean, and South America (Colombia) (Fig. 3a). Elevation 200–2850 m.

Ecology. On fallen, decaying logs, tree trunks or exposed roots of living trees, and less frequently on soil.

Discussion. The typical form of this species is distinct in its long-acuminate, often sharply serrate, flexuose leaf apices, and lanceolate or oblong-lanceolate leaves. The typical form has upper marginal cells that are wider and slightly longer than the adjacent median cells. These cells form what appears to be a border of enlarged cells along the upper leaf margins. *Rhynchostegiopsis flexuosa* is commonly found with sporophytes, even though it is dioicous. The typical form of *R. flexuosa* is most likely to be confused with *Leucomium*. It is similar in habit to *Leucomium strumosum*, but the serrate margins of *R. flexuosa* distinguish these species. Both species are similar in habit to some members

of the Hypnaceae, such as *Vesicularia*, but the absence of pseudoparaphyllia, undifferentiated alar cells, the two-celled axillary hairs, and distinct stem anatomy are characters that align them instead with the Hookeriales and/or the Leucomiaceae.

Within the genus *Rhynchostegiopsis* it is difficult to confuse the typical form of *R. flexuosa* with any of the other four species because of its small, narrow, lanceolate leaves; sharply serrate leaf margins; and long-acuminate, flexuose leaf apices. However, *R. flexuosa* is the most common and variable of the species in *Rhynchostegiopsis*. Variability is found in plant size, leaf size, leaf shape, apex length, the size of serrations, and the degree to which the apex is flexed. A rather confusing degree of variation is seen in a group of Central American specimens, mainly from Honduras and Belize. These plants have various combinations of the following characters that are different than the typical form of *R. flexuosa*: almost straight apices; short apices; only slightly serrate leaf margins; marginal cells similar in size to the adjacent median cells; or larger more ovate leaves. These specimens are often larger than the more typical forms of *R. flexuosa*, instead being more similar in size to plants previously known as *R. lutescens* (= *R. tunguraguana*). It is difficult to break down character variation seen in these plants in any informative way, since specimens that differ in one character can be typical for all others. For example, a specimen of *R. flexuosa* may have small, narrow, lanceolate leaves, marginal cells that are well developed, and serrate leaf margins, but with apices that are either non-flexuose or approach the short-acuminate form.

In this work, *Rhynchostegiopsis auricolor*, *R. cupressina*, and *R. serrata* remain in synonymy with *R. flexuosa*. The species *Rhynchostegiopsis auricolor*, first described as *Vesicularia auricolor*, was confirmed as being *R. flexuosa*. Plants from Mexico, previously named *Rhynchostegium cupressina* (*Rhynchostegiopsis cupressinum*), including the type specimen (*Sallé s.n.*, BM, NY) and a collection made by Pringle (*Pringle 10481* from BM, F, MO, NY, US), have slightly more ovate leaves with shorter, non-flexuose apices than the typical form of *R. flexuosa* (see leaf variation in Fig. 7b). However, their median cells, marginal cells, and serrate leaf margins are typical of *R. flexuosa*, supporting the synonymy of *R. cupressina* with *R. flexuosa*. *Rhynchostegiopsis serrata*, first described as *Leucomium serratum*, was differentiated from *R. flexuosa* by its autoicous sexuality and short seta length (Brotherus, 1907). The setae of *R. flexuosa* are characteristically long, but a degree of variation in the length

of setae was observed, particularly in specimens that were depauperate. Type material of *Leucomium serratum* was sterile, thus sexual condition could not be determined. In all other characters these plants were identical to *R. flexuosa*. Welch (1972) considered material of *R. serrata* from Guadeloupe, *Marie 652, 664* (BM, NY), and St. Vincent, *Morton 5506* (US), to be distinct from *R. flexuosa* because of their smaller size, serrate rather than sharply serrate upper leaf margins, and less flexuose leaf apices. However, none of these characters support *R. serrata* as a separate taxon.

Selected specimens examined. MEXICO. **Chiapas:** Pueblo Nueva, ca. 2000 m, *Sharp et al. 4209* (F, MO, US). **Guerrero:** 31 km N of El Paraiso, 2000 m, *Thomas & Contreras 3765* (NY). **Hidalgo:** Zacualtipan, 2100 m, *Sharp et al. 1872* (F). **Jalisco:** slopes of La Ferreria, *Crum 1068* (F, NY). **Oaxaca:** 15 mi. above Valle Nacional, *Sharp et al. 4520* (MO, F). **San Luis Potosí:** W of Xilitla, ca. 1200 m, *Sharp 5966* (US). **Veracruz:** Agua de la Calabaza, 1800 m, *Juarez 1046* (MO). BELIZE. **Cayo:** Doyle's Delight, 1098 m, *Allen 15122* (MO). **Toledo:** Southern Maya Mountains, 1000 m, *Allen 15464* (MO). GUATEMALA. **Alta Verapaz:** Samac, ca. 1400 m, *Johnson 794* (NY, US). **Baja Verapaz:** along dirt road 4 mi. NE of Purulhá, 1500 m, *Croat 41305* (MO). **Chimaltenango:** slopes of Volcán Acatenango, 2400–2700 m, *Standley 61818* (F, MO). **Huehuetenango:** Sierra de los Cucumatanes, 1500 m, *Steyermark 20056* (MO). **Quetzaltenango:** Volcán de Zumil, 2850 m, *Standley 64444* (MO). **San Marcos:** El Porvenir near Volcán Tajumulco, 1400 m, *Sharp 5372* (MO). **Suchitepequez:** Volcán Santa Clara, 1250–2650 m, *Steyermark 46711* (F). **Zacapa:** Río Sito Nuevo, 1500–1800 m, *Steyermark 43226* (F, NY). EL SALVADOR. **Santa Ana:** trail to the top of Monte Cristo, ca. 2300 m, *Watson ES-0022* (MO). HONDURAS. **Atlántida:** Lancetilla Valley, 200–600 m, *Standley 54633* (BM, F, NY, US). **Comayagua:** San Juanillo, 1700–2000 m, *Liesner 26810* (MO). **Copán:** El Zapote, 900B1000 m, *Allen 17768* (MO). **Cortés:** summit of Cerro Cantiles, 1600–2000 m, *Allen 14198* (MO). **Francisco Morazán:** Cerro de Uyuca, 1600 m, *Standley 4805* (F, MO). **La Paz:** Las Trances, 2000–2100 m, *Liesner 26479* (MO, NY). **Lempira:** Montana de Claque, 2040 m, *Allen 11263* (MO, NY). **Olancho:** La Muralla Biological Reserve, 1415 m, *Allen 12497* (MO). **Santa Bárbara:** E slope of Mt. Santa Barbara, 2220–2640 m, *Allen 11632* (MO). **Yoro:** Cordillera Nombre de Dios, ca. 300–400 m, *Allen 133615* (MO). NICARAGUA. **Jinotega:** N slope of Volcán Yali, 1200–1400 m, *Stevens & Grijalva 15265* (MO). COSTA RICA. **Alajuela:** Viento Fresco, 1600–1900 m, *Standley & Torres 47877* (US). **Cartago:** El Muñeco, 1400 m, *Standley 33697* (NY, US). **Guanacaste:** Parque Nacional de Guanacaste, 700 m, *Chávez 73* (MO). **Heredia:** Porrosati Area, 2250 m, *Crosby & Crosby 6021* (MO). **San José:** San Maria de Data, 1800 m, *Standley 42934b* (US). PANAMA. **Bocas del Toro:** on hwy. to Chiriquí Grande, 250–300 m, *Allen 5542* (MO). **Chiriquí:** Volcán Barú, 1750–1900 m, *Almeda 6197* (MO). **Darién:** Cana, 800–1200 m, *Allen 8843* (MO, NY). CUBA. Locality not indicated, *Wright 112 & 113* (BM, NY). **Potosí:** Monte Toro, *Wright 173* (MO). **San Juan:** San Juan, *Hioram 12539* (MO). JAMAICA. **St. Thomas:** Cuna Cuna

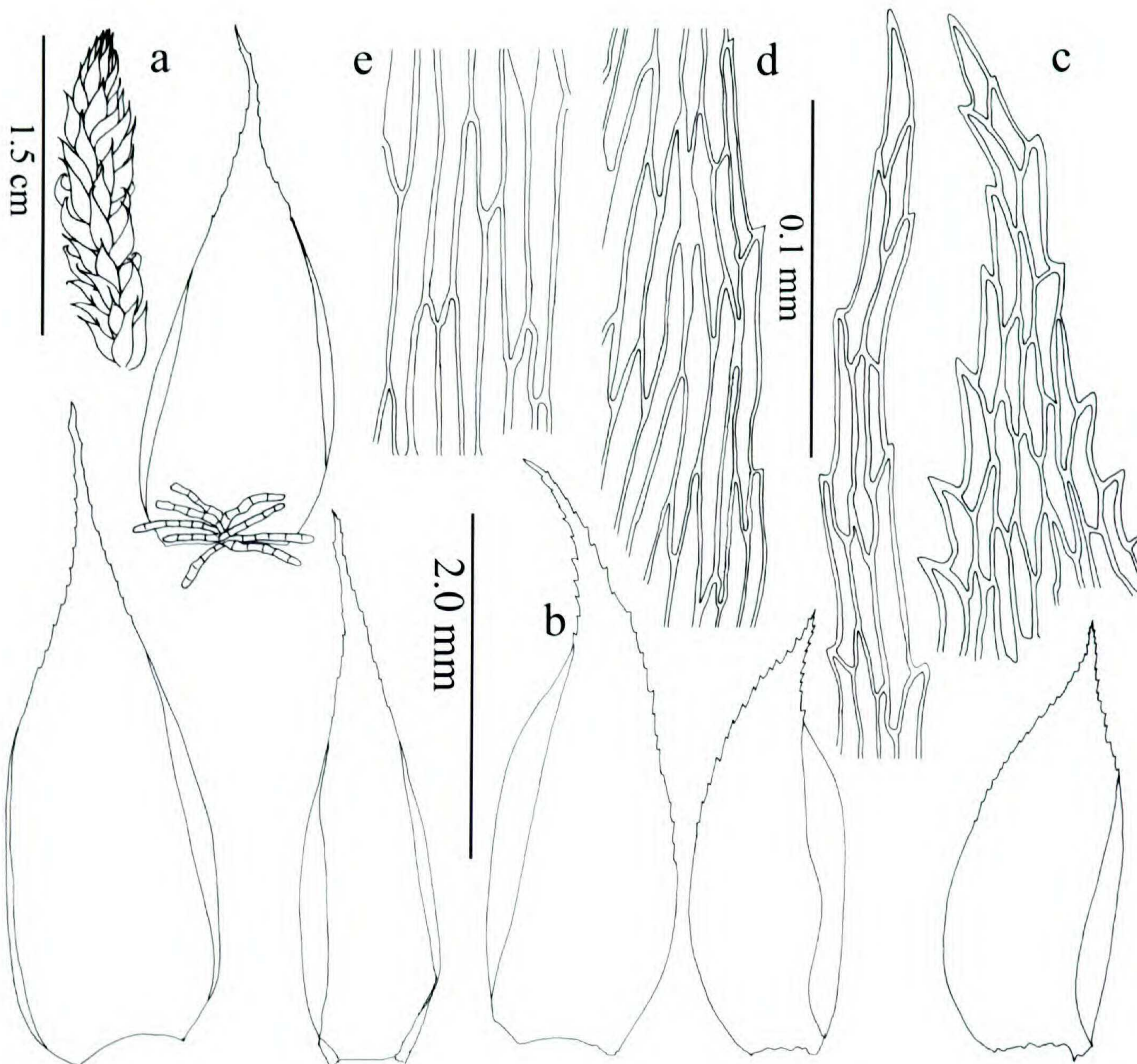


Figure 8. *Rhynchosstegiopsis tunguraguana*. —a. Portion of stem. —b. Leaves. —c. Leaf apices. —d. Leaf margin. —e. Median cells. (a, c–e: *Spruce 1048*, NY, holotype; b: *Lewis 83–710*, LPB, *Britton 1142*, NY, *Spruce 1048*, NY, holotype.)

Trail, *Maxon & Killip 163* (BM, F, NY, US). DOMINICAN REPUBLIC. **La Vega**: Constanza, ca. 1500 m, *Buck 7909* (NY). TRINIDAD. Locality not indicated. *Cruger s.n.* (BM, NY). PUERTO RICO. **Las Piedras**: El Toro, 400–550 m, *Price 834* (MO). GUADELOUPE. Locality not indicated, *Hooker 190* (NY); Route du Gommier, sur les troncos pourris, *Ed. Marie 664* (syntypes of *L. serratum*, BM!, NY!). DOMINICA. Morne Micotrin, ca. 1000 m, *Elliot 22* (BM). ST. VINCENT. Cumberland River, 400–600 m, *Morton 5506* (US). COLOMBIA. **Meta**: Villavicencio, 765–1080 m, *Steere 7671* (MO, NY).

5. *Rhynchosstegiopsis tunguraguana* (Mitt.) Broth., in Engl. & Prantl, *Nat. Pflanzenfam.* I(3): 1235. 1909. *Stereodon tunguraguanus* Mitt., *J. Linn. Soc., Bot.* 12: 534. 1869. TYPE: Ecuador. “Andes Quitensis, in monte Tunguragua supra pagum Puela, 6000 ped.” *R. Spruce 1048* (holotype, NY!; isotypes, BM!, H-BR!). Figure 8.

Rhynchosstegiopsis complanata Müll. Hal., *Nuovo Giorn. Bot. Ital.* n.s. 4: 163. 1897. No specimen cited. TYPE: Bolivia. Based on: “Cochabamba: prope Choquecamata, June 1889,” *P. Germain 1147* (lectotype, here designated, NY!; isolectotype, H-BR!).

Rhynchosstegiopsis lutescens E. Britton, in Broth., in Engl. & Prantl, *Nat. Pflanzenfam.* (ed. 2) 11: 263. 1925. No specimen cited. TYPE: Jamaica. Based on: “St. Andrew: Slopes of Sir John and summit, Blue Mountains, 5 Oct. 1908,” *E. G. Britton 1142* (holotype, NY!; isotypes, BM!, H-BR!); see Crum & Bartram (1958).

Rhynchosstegiopsis planifolia H. A. Crum & E. B. Bartram, *Bull. Inst. Jamaica* 8: 55. 1958. Nom. illeg. incl. sp. prior. TYPE: “Jamaica. St. Thomas: Terrestrial, moist bank in montane rain forest, 6000 ft., Blue Mountain Peak track, 16 Dec. 1951,” *R. G. Robbins 89* (holotype, FH not seen; isotype, US!).

Plants medium to large, robust, pale yellow-green to golden; forming dense to sparse mats.

Stems 35–70(–100) × 2–5 mm, stems sometimes fragile, creeping or spreading, infrequently sub-pinnately branched. *Leaves* slightly folded when dry, folded when wet, complanate to spreading, often falcate with leaf apices pointing to substrate, usually crowded, slightly dimorphic, ovate to ovate-lanceolate, 1.7–4.6 × 0.7–1.6 mm, leaves concave below, plane above; apices short- or long-acuminate, sometimes flexuose; margins entire below, serrate to serrulate above; upper marginal cells, not or slightly larger than median cells, 50–200 × 6–20 μm; median cells long-linear, 52–288 × 8–37 μm; basal cells usually shorter and broader than median cells, 52–157 × 17–40 μm. *Asexual reproduction* infrequent, gemmae at base of leaf, not prominent, slightly orange colored at base, hyaline above, up to 8 cells long. *Perigonia* lateral, inconspicuous. *Perichaetia* lateral, conspicuous, leaves 0.7–1.9 mm, short- or long-acuminate from an ovate base, apices serrulate to sub-entire. *Setae* 20–25 mm, smooth reddish to dark red. *Capsules* inclined; *urn* ovoid-cylindrical, 2–2.5 × 0.5–1.4 mm; *annuli* not seen; *opercula* long-rostrate, 1.5 mm; *exostome teeth* 500–600 μm. *Calyptra* 3.8 mm. *Spores* 12–19 μm diam.

Etymology. Derived from its collection locality in Ecuador.

Illustrations. Crum (1994), figure 630; Churchill and Linares (1995), figure 119; Buck (1998), plate 36.

Distribution. Mexico, Central America, the Caribbean, and South America (Fig. 2). Elevation 600–3450 m.

Ecology. On roots, trunks, or branches of living trees, rotting logs, leaf litter, and moist shaded terrestrial habitats such as road banks, ravines, and drainage ditches.

Discussion. This species is best distinguished by its habit with complanate, leafy stems, and leaves with apices that often point downward. The leaves of *R. tunguraguana* are ovate to ovate-lanceolate with either gradually long- or short-acuminate apices. Larger specimens of *R. tunguraguana* may be confused with *R. carolae*, but they can be separated by their leaf apices, more crowded leaves, length of median cells, and the size of marginal cells. Only one calyptra of *R. tunguraguana* was seen during this study, Churchill & Sastre de Jesus 12999 (NY), and it was longer than the calyptrae seen in specimens of *R. carolae*. The calyptra of *R. tunguraguana* was 3.8 mm, while those seen in *R. carolae* were up to 2 mm in length. *Rhynchostegiopsis tunguraguana* has been found with gemmae at the base of the leaf, a character previously thought to

be found exclusively in *R. costaricensis*. The gemmae in *R. tunguraguana* are more loosely arranged, much shorter, and less well developed than those seen in *R. costaricensis*; see discussion under *R. costaricensis* (Figs. 6, 8).

Examination of plants from the Caribbean, Central America, and South America revealed a pattern of continuous character variation in *R. lutescens*, *R. complanata*, and *R. tunguraguana*. Plants from Jamaica, the Dominican Republic, and Central America, previously known as *R. lutescens*, often have shorter, more sharply serrate leaf apices than the South American plants. However, they are similar in all other characters to *R. tunguraguana*. The name *R. lutescens* had been previously placed under the synonymy of *R. tunguraguana* (Crum, 1994; Buck, 1998), which is upheld in this work. Plants from Bolivia, earlier identified as *R. complanata*, have very long-acuminate, sometimes flexuose leaf apices, and marginal cells that form a border. Their long-acuminate, sometimes flexuose leaf margins are similar to those of *R. flexuosa*, but their much larger size and larger leaf cells distinguish them from this species. In all other characters, *R. complanata* falls within the variation of *R. tunguraguana* and is maintained in synonymy of it.

There has been some confusion over the validity and use of the names *Rhynchostegiopsis lutescens* and *R. planifolia* (Welch, 1971). *Rhynchostegiopsis lutescens* was published with a minimal description by E. G. Britton in Brotherus (1925). This name was incorrectly cited as being a nomen nudum by Crum and Bartram (1958), who placed it in synonymy of their newly described *R. planifolia*. In the herbarium at The New York Botanical Garden, the specimen Britton 1142 ascribed to *R. lutescens* includes a lengthy description of this species and illustrations of the plant by E. G. Britton, presumably intended for publication. Although no type was cited for this species in the original publication (Brotherus, 1925), this specimen has been considered to be the type based on the presence of the unpublished manuscript with the herbarium sheet (Crum & Bartram, 1958). The description of *R. planifolia* by Crum and Bartram (1958) was based on some of the same specimens that had been examined by E. G. Britton, including the putative type (Britton 1142, NY) and two other specimens from Jamaica (Nichols 179 & 184, both NY), which were then included in the protologue of *R. planifolia*. The description of *R. planifolia* incorporated parts taken from the unpublished manuscript of E. Britton (Crum & Bartram, 1958). Although *R. planifolia* was based on a different type specimen (Robbins 89, FH, US) it is an illegitimate name because

it included the valid prior name *R. lutescens*. Welch (1971) used the name *R. planifolia* based on the assumption that *R. lutescens* was not validly published, because it lacked a Latin diagnosis. However, a Latin diagnosis was not required at the time of publication of the original article. Wijk et al. (1967) correctly treated the name *R. planifolia* as an illegal name.

Selected specimens examined. MEXICO. **Oaxaca:** S of Valle Nacional, ca. 3000 m, *Whittemore 1889A* (MO). BELIZE. **Toledo:** Columbia River Forest Reserve, 600–700 m, *Allen 18539* (MO). COSTA RICA. **San José:** Las Nubes, *Wendland s.n.* (BM, NY). HONDURAS. **Francisco Morazán:** El Parque Nacional la Tigra, 2000 m, *Allen 12368* (MO). **Lempira:** Montaña de Celaque, 2250 m, *Allen 12219* (MO). **Ocotepeque:** Nueva Ocotepeque, 2000–2180 m, *Allen 14452* (MO). **Olancho:** Montaña Babilonia, *Allen 12713* (MO). JAMAICA. **St. Andrew:** Sir John Peak, *Nichols 179 & 184* (NY). **St. Thomas:** Blue Mountains, Morce's Gap, *Nichols 37* (BM). DOMINICAN REPUBLIC. **La Vega:** La Nevera, 2100 m, *Buck 5395* (NY). VENEZUELA. **Trujillo:** Páramo de Guaramacal, 2800 m, *Dorr et al. 5034* (NY). COLOMBIA. **Antioquia:** Alto de Boguerón, 2800–3000 m, *Churchill et al. 14255* (MO). **Cauca:** Cerro Munchique, 2300–2555 m, *Churchill & Betancur 18150* (MO, NY). **Magdalena:** Río Buritaca, 2700 m, *Cleef et al. 302* (MO). **Nariño:** Alto Zapallurco, 3250 m, *Ramírez & Salas 10863* (MO). **Putumayo:** Reserva Natural La Rejoia, 2750 m, *Ramírez 10205* (MO). ECUADOR. **Carchi:** La Estrellita, 3300 m, *Dorr & Barnett 6149* (NY). **Chimborazo:** Puela, 1850 m, *Spruce 1048* (BM, NY). **Imbabura:** Lago San Marcos, 3450 m, *Cazalet & Pennington 52* (NY). **Loja:** Cajanuma, 2800 m, *Laegaard & Luzano 18518* (MO). **Napo:** Guagra Urcu, 2800 m, *Holm-Nielsen et al. 27339* (MO). **Sucumbios:** San Gabriel, 21501–2615 m, *Steere 9133* (NY). BOLIVIA. **Cochabamba:** Río Tocarani, 2200 m, *Herzog 4025* (BM, MO, NY). **La Paz:** Chusipata, ca. 2950 m, *Lewis 83–710* (LPB).

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APPENDIX I

LIST OF SPECIES

1. *Rhynchostegiopsis brasiliensis* Broth.
2. *Rhynchostegiopsis carolae* Crosby
3. *Rhynchostegiopsis costaricensis* H. Rob. & D. G. Griffin
4. *Rhynchostegiopsis flexuosa* (Sull.) Müll. Hal.
5. *Rhynchostegiopsis tunguraguana* (Mitt.) Broth.

INDEX TO SPECIMENS EXAMINED

Specimens examined are listed below alphabetically by collector. Records include collection number and herbarium locations for each specimen. The species is indicated by a number in parentheses corresponding to the number in the List of Species.

Acuña 450 (DUKE) (4), 452 (DUKE, NY) (4); Allard 18624 (US) (4), 18753 (NY) (4); Allen 5542 (MO) (4), 5820 (MO) (4), 8843 (MO, NY) (4), 8869 (MO) (4), 11041 (MO) (4), 11043 (MO) (4), 11051 (MO) (4), 11054 (MO) (5), 11061 (MO) (5), 11067 (MO) (5), 11068 (DUKE, MO, NY) (5), 11072 (MO) (4), 11081 (MO) (5), 11209 (MO) (4), 11263 (MO, NY) (4), 11267 (MO) (4), 11309 (MO) (4), 11315 (MO) (4), 11373 (MO) (4), 11374 (MO) (4), 11377 (MO) (4), 11392 (MO) (4), 11404 (MO) (4), 11421 (MO) (4), 11470 (MO) (3), 11525 (MO) (4), 11526 (MO) (4), 11615 (MO) (4), 11632 (MO) (4), 11923 (DUKE, MO) (4), 11924 (MO) (4), 11925 (MO) (4), 11959 (MO) (4), 12028 (MO) (4), 12040 (MO) (5), 12042 (MO) (4), 12060 (MO) (5), 12064 (MO) (5), 12112 (DUKE, MO) (4), 12218 (MO) (4), 12219 (MO) (5), 12259 (MO) (4), 12285 (MO) (5), 12318 (MO) (5), 12325 (MO) (4), 12343 (MO, NY) (4), 12363 (MO) (4), 12368 (MO) (5), 12369 (MO) (4), 12497 (MO) (4), 12567 (MO) (4), 12571 (MO) (4), 12588 (MO) (4), 12670 (MO) (4), 12713 (MO) (5), 12855 (MO) (4), 12869 (MO) (4), 13615 (MO) (4), 13618 (MO) (4), 13775 (MO) (4), 13791 (MO) (4), 13792 (MO) (4), 13816 (MO) (4), 13901 (MO) (4), 13902 (MO) (4), 14198 (MO) (4), 14199 (MO) (4), 14206 (DUKE, MO) (4), 14326 (MO) (4), 14399 (MO) (4), 14452 (MO) (5), 14481 (MO) (5), 14504 (MO) (5), 14547 (MO) (5), 15101 (MO) (4), 15122 (MO) (4), 15126 (MO) (4), 15139 (DUKE, MO) (4), 15158 (MO) (4), 15334 (MO) (4), 15353 (MO) (4), 15395 (MO) (4), 15420 (MO) (4), 15464 (MO) (4), 15479 (MO) (4), 17329 (MO) (4), 17580 (MO) (4), 17581 (MO) (4), 17730 (MO) (4), 17768 (MO) (4), 17760 (MO) (4), 17772 (MO) (4), 18527 (MO) (4), 18539 (MO) (5), 18597 (MO) (4),

18603 (MO) (4), 18605 (MO) (4), 18651 (MO) (4), 18710 (MO) (4), 18986 (MO) (4), 19006 (MO) (4); Almeda & McPherson 6197 (MO) (4); Antonio 1432 (MO) (2); Araya & Griffin 81 (DUKE, F, MO, NY, US) (3).

Barnes & Land 572 (H, NY) (4), 585 (NY) (4); Breedlove 25021 (MO) (4), 25024 (MO) (4), 29980a (MO) (4); Britton 379 (NY) (4), 1142 (BM, DUKE, H, H-BR, NY) (5), 3982 (NY) (4), s.n. (BM) (5); Buck 5303 (NY) (5), 5563 (NY) (4), 5644 (NY) (4), 7604 (H, NY) (4), 7610 (NY) (4), 7909 (NY) (4), 8674 (NY) (5).

Callejas & Roldán 10618 (NY) (5); Callejas et al. 10110 (MO, NY) (5); Carlson 2486 (F) (4); Cazalet & Pennington 52 (NY) (5); Chaney s.n. (US) (4); Chávez 73 (MO) (4); Churchill & Betancur 18128 (NY) (5), 18150 (MO, NY) (5), 18664 (NY) (5), 18667 (NY) (5), 18673 (NY) (5), 18689 (MO, NY) (5), 18741 (MO, NY) (5); Churchill & Marulanda 15729 (NY) (5); Churchill & Rengifo 17496 (NY) (5), 17499 (NY) (5); Churchill & Sastre de Jesús 12903 (NY) (5), 12986-b (NY) (5), 12906 (DUKE, MO, NY) (5), 12990-b (MO, NY) (5), 12999 (NY) (5); Churchill et al. 14255 (H, MO, NY, US) (5), 14263 (NY) (5); Cleef et al. 302 (MO) (5); Clement 14535 (NY) (4); Clements 14 (NY) (4); Cook & Griggs 93 (NY, US) (4); Croat 41305 (MO) (4), 43391 (MO) (4); Crosby 2840 (MO) (4), 3203 (DUKE, MO) (4), 3415 (DUKE, MO) (5), 3429 (MO) (4), 3517 (DUKE, MO) (5), 3989 (MO) (4), 3704 (MO) (2), 9754 (MO) (3), 9761 (MO) (2), 9766 (MO) (2), 9789 (MO) (3), 9860 (MO) (5), 9928 (MO) (4), 9980 (MO) (4), 10109 (MO) (4), 10300 (MO) (4), 10861 (MO) (2), 10932 (MO) (2), 13128 (MO) (3), 13142 (MO) (2), 13771 (NY) (4), 13793 (NY) (4); Crosby & Crosby 5849 (DUKE, MO) (4), 5957 (MO) (2), 6005 (MO) (2), 6117 (DUKE, MO) (3), 6604 (MO) (3), 6608 (MO) (2), 8567 (MO) (4), 5836 (BM, DUKE, MO, NY) (2), 5860 (MO) (4), 6021 (MO) (4), 8523 (MO) (2); Crüger s.n. (NY, BM) (4); Crum 1068 (F, NY) (4).

Davidse & Zúñiga 34760A (MO) (4); Delgadillo 1257 (MO) (4); Dorr & Barnett 6149 (NY) (5); Dorr et al. 5034 (NY) (5); Duncan s.n. (MO) (4); Duss 394 (NY) (4).

Elliot 7a (BM) (4), 8a (BM) (4), 22 (BM) (4), 69c (BM) (4), 98a (BM) (4), 1983 (BM) (4).

Germain 1147 (H-BR, NY) (5); Griffin et al. 92 (US) (3).

Hattaway et al. 112 (F, MO) (4); Herzog 4025 (BM, JE, MO, NY, PC) (5); Hioram 11940 (BM, F) (4), 12539 (F, MO) (4), 12699 (F) (4), 12757 (F) (4), 13620 (F) (4), 13697 (F) (4), 13756 (F) (4); Holm-Nielsen et al. 26952 (MO, NY) (5), 26962 (MO, NY) (5), 27145 (MO) (5), 27339 (MO, NY) (5); Holst 5831 (MO) (4), 5832 (MO) (4); Hooker 190 (NY) (4).

Johnson 794 (NY, US) (4); Juarez 981 (MO) (4), 1046 (MO) (4).

King C91–91 (MO) (4).

Laegaard 53628H (NY) (5); Laegaard & Luzano 18518 E (MO) (5); Leon 14559 (NY) (4); Leon & Clements 5476a (NY) (4); Lewis 83–710 (LPB) (5), 83–715 (LPB) (5); Liesner 26479 (MO, NY) (4), 26810 (MO) (4); Lyon 387 (MO) (4), 389 (MO) (4).

Marie 652 (NY) (4), 654 (NY) (4), 664 (BM) (4); Matuda s.n. (DUKE) (4); Maxon 9354 (MO, NY) (4); Maxon & Killip 160 (BM, F, NY, US) (4), 163 (BM, F, NY, US) (4); McPherson 13251D (MO) (5); Morton 7215a (US) (4); Morales 21429 (US) (3); Morales & Griffin 38 (MO) (3); Morton 5506 (US) (4), 7195 (US) (4), 7382 (US) (4), 7395 (US) (4), 9441 (US) (4); Morton & Acuña 3649 (US) (4); Murrill & Murrill 29 (NY) (4).

Nichols 37 (BM) (5), 179 (NY) (5), 184 (BM, NY) (5).

s.n. (DUKE) (5); Norris et al. 5613 (NY) (5), 5614 (NY) (5).

Olson 84-49a (MO) (4), 84-53 (MO) (4); Orcutt 7015 (US) (4).

Patterson & Bartram 49A (NY) (5); Price 834 (MO) (4), 839 (MO) (4); Pringle 10481 (BM, F, MO, NY, US) (4); Proctor 31252 (MO) (4).

Ramírez 2946 (NY) (5), 3056 (MO) (5), 10118 (MO) (5), 10205 (MO) (5), 10932 (MO) (5); Ramírez et al. 9039 (MO) (5), 10381 (MO) (5), 10405 (MO) (5); Ramírez & Salas 10863 (MO) (5); Reese 15745 (NY) (5); Richards & Sharp 7020 (F) (4); Robbins 89 (US) (5).

Salazar 694 (NY) (4); Salle s.n. (NY) (4); Schiffner 679 (BM) (1), 1122 (BM, H-BR) (1), 1454 (BM, H-BR) (1); Sharp 918 (US) (4), 2750 (US) (4), 3184 (US) (4), 3473 (US) (4), 3792-a (MO) (5), 3798 (F) (4), 3812-a (DUKE, F) (4), 5372 (DUKE, MO) (4), 5558 (US) (4), 5966 (US) (4), M59153 (US) (4), s.n. (US) (4), s.n. (US) (4); Sharp et al. 99-a (F) (4), 1863 (F) (4), 1872 (F) (4), 2831 (MO) (4), 3090 (F) (4), 4079 (F) (4), 4138 (F) (4), 4197 (F, MO) (4), 4207a (F) (4), 4209 (DUKE, F, MO, US) (4), 4367-f (F) (4), 4375 (MO) (4), 4507-b (MO) (4), 4520 (F, MO) (4); Shaw 5103 (NY) (4), 5765 (NY) (5); Smith et al. 2839 (F, MO) (4), 3079 (F) (4), 3117 (MO) (4); Spruce 1048 (BM, NY, H-BR) (5); Standley 4805 (BM, F, MO) (4), 4893 (F) (4), 4940 (F, MO) (4), 4954 (F) (4), 14112 (F) (4), 15659 (F) (4), 20676 (F) (4), 33697 (NY, US) (4), 42934b (US) (4), 47824 (NY, US) (4), 51185 (US) (4), 51185c (US) (4),

52598 (US) (4), 52898 (F) (4), 54633 (BM, F, NY, US) (4), 54644 (F, US) (4), 61818 (MO, F) (4), 64444 (MO) (4), 67444 (F) (4), 67450 (MO) (5), 67458 (F) (5), 67878 (F) (4), 70410a (F) (4), 80525 (F) (4), 85021 (F, NY, US) (4), 85022 (F) (4), 85024 (F) (4), 85577 (F) (4), 85926 (DUKE, F) (5), 85983 (F) (4), 85994 (F, NY) (5), 86406 (F, NY) (4), 91963 (F) (4); Standley & Torres 47592 (US) (4), 47653 (US) (4), 47877 (US) (4); Standley & Williams 707 (F) (4), 708a (F) (4); Steere 7668a (NY) (4), 7671 (MO, NY) (4), 9133 (NY) (5), 23073 (NY) (5), J-28 (NY) (4), J-86 (NY) (4); Stehle 7226 (US) (4); Stevens & Grijalva 15263 (MO) (4), 15265 (MO) (4); Steyermark 20056 (MO) (4), 31009 (DUKE, F, MO) (4), 33645 (F) (4), 33646 (F) (4), 34090 (F, NY) (5), 34324 (F) (4), 41919 (F) (4), 42557 (F) (4), 42656 (F) (4), 42660 (F) (4), 42661 (F) (4), 43226 (F, NY) (4), 46711 (F) (4), 48866 (F) (4), s.n. (NY) (4); Steyermark et al. 100692 (US) (5).

Thomas & Contreras 3765 (NY) (4); Thomas et al. 3571 (NY) (4); Türkheim 7374 (NY) (4), 7478 (BM) (4), 7507 (DUKE, NY) (4), s.n. (H-BR) (4).

Underwood 3377 (BM, NY, US) (4); Underwood & Earle 911 (NY, US) (4), s.n. (F) (4).

Watson ES-0022 (MO) (4); Wendland s.n. (BM, NY) (5), s.n. (BM) (5); Whittmore 1889A (MO) (5); Wright 112 (BM, H-BR, NY) (4), 113 (BM, NY) (4), 170 (NY) (4), 173 (DUKE, F, MO, US) (4).

Zanoni & Pimentel 20893T (MO, NY) (5); Zanoni et al. 25065-B (NY) (4).

RADIATION OF POLLINATION SYSTEMS IN *GLADIOLUS* (IRIDACEAE: CROCOIDEAE) IN SOUTHERN AFRICA¹

Peter Goldblatt,² John C. Manning,³ and Peter Bernhardt⁴

ABSTRACT.

Pollination strategies adopted by the largely sub-Saharan African *Gladiolus* (approximately 260 species), one of the largest genera of the monocot family Iridaceae, are unusually diverse. The primary or sole pollinators include long-tongued apid and anthophorine bees (Apidae), short-tongued halictid and andrenid bees (Halictidae, Andrenidae), sometimes in combination with hopliine beetles (Scarabaeidae), long-proboscid flies (Nemestrinidae, Tabanidae), large butterflies (Satyridae), moths (mostly Noctuidae and Sphingidae), and sunbirds (Passerinae). Floral form correlates closely with pollination strategy, allowing us to infer the pollination ecology of almost all 165 species in southern Africa, although we have observations of animal visitors capable of accomplishing pollen transfer in only half this number. Pollination by apid bees foraging for nectar and passively transferring pollen brushed onto their bodies during feeding occurs in all seven sections of the genus in southern Africa and is also the most common strategy in five of these sections. Other pollinators include female bees actively foraging for pollen, or long-proboscid flies, sunbirds, moths, the satyrid butterfly, *Aeropetes*, all foraging for nectar, and in one species hopliine beetles that use the flowers as sites for assembly and copulation. Shifts in floral form associated with changes in pollination appear complex in the large flowers of *Gladiolus* species, but may in fact involve relatively simple developmental modifications, involving changes in perianth pigmentation, and often the type of marking on the tepals, presence or absence of scent, length of the perianth tube, and occasionally a shift from zygomorphy to actinomorphy. Associated with these changes is a correlated adjustment in nectar characteristics, including volume, sugar concentration, and sometimes sugar chemistry. With an inferred minimum of 32 shifts in pollination system in the 165 species in southern Africa, *Gladiolus* appears to have an unusually labile floral morphology, which may account for its extensive adaptive radiation.

Key words: bees, butterflies, floral ecology, *Gladiolus*, Iridaceae, long-proboscid flies, moths, nectar, pollination systems, sunbirds.

The pollination ecology of most genera of African Iridaceae is remarkably diverse (Bernhardt & Goldblatt, 2000). For example, in *Sparaxis* four different pollination systems have been described in 13 of its 15 species studied (Goldblatt et al., 2000a). In general, the larger the genus the greater the diversity of pollination systems. Thus, in *Lapeirousia* (Goldblatt et al., 1995), with almost half the species in the genus studied, five different pollination systems have been identified among 20 species. For the genus *Ixia*, with an estimated 50 species, six different systems have been described for 20 species (Goldblatt et al., 2000b). The genus *Gladiolus*, with some 255 species in Africa, is thus a primary target for the analysis of pollination systems as it is the largest genus in the family in Africa (Goldblatt, 1996; Goldblatt & Manning, 1998).

Seven distinct and, with few exceptions, non-overlapping pollination systems (Table 1) occur

among the 80 *Gladiolus* species studied to date, which suggests that the range of pollination systems in *Gladiolus* may be wider than in any other genus of the Iridaceae in Africa and probably in the entire family. A general review comparing the pollination systems in *Gladiolus* is useful for two reasons. First, as usual, significant literature is scattered throughout technical journals, popular publications, and scientific monographs. Second, because widely different pollination systems occur in closely related species, a review of pollination in *Gladiolus* may make a useful model system for expanding our understanding of the adaptations associated with pollination shifts and how often pollination mechanisms change within a plant lineage.

Gladiolus is believed to be monophyletic, as circumscribed by Goldblatt and Manning (1998). It is defined largely on non-floral characters, the flowers being highly variable as they reflect direct adap-

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